14
From the Dust Bowl to the Green Glacier: Human Activity and Environmental Change in Great Plains Grasslands

David M. Engle, Bryan R. Coppedge, and Samuel D. Fuhlendorf

Introduction

Before European settlement, the land between the Rocky Mountains and the Mississippi River of North America formed immense unbroken grasslands devoid of trees except those few forming gallery forests along lower river channels and those located in disjunct topoedaphic sites protected from fire. The Great Plains grasslands are now extensively fragmented by cropland agriculture, human occupation, and woody plant encroachment and altered directly and indirectly by livestock grazing and other anthropogenic disturbances. As a consequence of these processes, today's grasslands bear little resemblance to those of pre-European settlement and are now recognized as one of the most endangered ecosystems in North America (Sampson and Knopf 1994). Awareness of the unique biodiversity of the Great Plains and its importance to our natural heritage has highlighted the need for a regional approach to conservation of remnant grasslands (Joern and Keeler 1995; Mitchell et al. 1999). In part, this need is urgent because many of the species endemic to the region are declining rapidly.

According to the North American Breeding Bird Survey, 70% of the 29 bird species characteristic of North American grasslands have declined between 1966 and 1993, and they are declining at a faster rate than any other guild of terrestrial birds in North America (Knopf 1994; Peterjohn and Sauer 1999). Although many factors have been suggested as contributing causes to the decline (Peterjohn and Sauer 1999), habitat fragmentation and degradation are generally recognized as central issues (Vickery et al. 1999). Cultivation was historically the primary factor fragmenting grasslands, but in most regions cultivated land has stabilized or even decreased over the past 20 years (Laycock 1988). The factor contributing most to the current decline in grassland habitat quality in the Great Plains is the expansion of woody plants, particularly eastern redcedar (*Juniperus virginiana* L.) (Coppedge et al. 2001a). In this chapter, we use population and community properties of the Great Plains avifauna to demonstrate that the spread of woody plants into grasslands, part of a broad process we call the *Green Glacier*, is changing endemic avifauna to an extent equivalent to that of the Pleistocene glaciation.

O.W. Van Auken (ed.), *Western North American Juniperus Communities: A Dynamic Vegetation Type.*

Environmental History and Development of Great Plains Grassland Fauna: The Great Change Events

Understanding the role of climate, drought, grazing animals, and fire on the development and evolution of Great Plains grasslands and associated avifauna is critical to interpreting many of the processes now affecting them. The development of these grasslands is largely attributed to the Miocene uplift of the Rocky Mountains that produced the rain shadow which limits moisture availability and increases the probability of prolonged droughts (Axelrod 1985). Because grasses are generally better adapted to drier conditions than woody plants, the spread of grasslands in the drier environment came at the expense of forests (Daubenmire 1978; Anderson 1990). Fire was a key process in the conversion of central North America from forests to grasslands, and fire remains critical for maintaining the dominance of herbaceous vegetation types (Axelrod 1985; Coupland 1992).

The region is now characterized by an east–west precipitation gradient and a south–north temperature gradient (Epstein et al. 1996). As moisture availability increases from west to east in the Great Plains, grasslands intergrade eventually into the eastern deciduous forests. In the eastern tallgrass prairie region where precipitation is adequate for trees, fire is critical in restricting woody plant intrusion into grasslands (Briggs et al. 2005). But fire plays a significant role even in the drier mixed prairie and shortgrass prairie, and woody plants have also increased in these regions in the absence of fire over most of the past century (Engle et al. 1996; Coppedge et al. 2001b).

Glaciers and Aboriginal Activity

No other recent geological or climatological event has shaped Great Plains fauna more than glaciation (Borchert 1950; Pielou 1992). During the development of grassland dominance at the initiation of the current interglacial period [10,000 to 15,000 years before present (B.P.)], most of the Pleistocene mammalian megafauna became extinct. These extinctions included mammoths, mastodons, camels, giant ground sloths, musk ox, horses, and the precursors to modern species of American bison (*Bos bison* L.). The modern bison form gained dominance in the absence of competition across the Great Plains after the last (Wisconsin) glaciation (McDonald 1981; Stebbins 1981; Mack and Thompson 1982).

Grassland dominance of central North America peaked about 7000 years ago (Wright 1970). Large herds of bison and frequent anthropogenic burning of grassland fuels within the past 5000 years (Pyne 1982; Anderson 1990) together augmented the influence of aridity on the development of Great Plains grasslands. Thus, the relatively young age of the Great Plains grasslands has resulted in an endemic avifauna that is comparatively depauperate (Knopf 1994), making their conservation even more urgent.

Drought, Sodbreaking by Europeans, and the Dust Bowl

Except for perhaps climate, the ecological processes governing Great Plains biota have been altered substantially during the past 150 years. Foremost in these processes is the substitution of native flora for cultivated monocultures. However, settlement and subsequent cultivation patterns varied across the Great Plains depending on soils, climate, and socioeconomic boundaries. Relatively flat topography, nutrient-rich soils, and government policies (e.g., the Homestead Act of 1862) invited and often encouraged cultivation on much of these lands. By the dawn of the 20th century, Euro-American settlement claimed most of the arable lands for cultivation in the Great Plains, and settlement integrated grazing agriculture into most of the remaining land in the region. Cycles of cultivation and cropland abandonment in the 20th century were punctuated periodically by federal conservation and incentive programs driven only in part by the goals of maintaining the productivity, sustainability, and economic viability of the region (Bedenbaugh 1988; Joyce 1989). Given the regional socioeconomic significance of cropland agriculture, drought continues to play havoc with the economic stability of the region (Albertson et al. 1957; Baltensperger 1979; Glantz 1994).

Severe drought plagued European settlers in the Great Plains following settlement, with the droughts of the 1890s, 1930s and 1950s indelibly marking the history of the Great Plains (Flores 1996; Licht 1997). The Dust Bowl, associated with ill-advised cultivation of the western Plains and the drought of the 1930s, is one of the greatest ecological disasters in the history of the United States. Sala et al. (1988) derived an index of variability in primary production, the difference between the maximum and minimum production in above-average and below-average precipitation years divided by the average production. An area centered around southwest Kansas, northwest Oklahoma, and into southeast Colorado and northeast New Mexico has a variability index of 0.9, meaning that fluctuations in forage production are 90% of the average. Much of the Great Plains, including all the states of Kansas and Oklahoma, has an index of 0.5 or more.

The Euro-American culture that settled the New World focused on removing most natural habitats, such as grasslands, forests, and wetlands, which were perceived as impediments to progress (Sopuck 1995). Limited species diversity, apparent monoculture over most of the region, and conversion to cropland agriculture of more than 80% of the landscape is evidence that these strategies have been effective. However, those areas on the Great Plains that escaped cultivation are dominated by vegetation very similar to the potential natural plant community described by Kuchler (1964; O'Neill et al. 1997), and are typically rangelands used for livestock production by private landowners. Because these areas are often extensively managed native plant communities surrounded by intensively managed cropland or pastureland, they are essential to conservation of the native biota of the Great Plains. Economic, social, and political pressures on these rangelands will continue to increase as ecological awareness in the general population grows and economic changes in agriculture also increase.

Eastern Redcedar: The Green Glacier

Juniper (*Juniperus* spp.) expansion is well documented in the Great Plains (Figure 1). Ashe juniper (*J. ashei*) and redberry juniper (*J. pinchotii*) have expanded in the extreme southern portion of the Great Plains (Ansley et al. 1995; Fuhlendorf et al. 1996), whereas eastern redcedar has expanded throughout the Great Plains, except the far north and far west areas (Van Haverbeeke and King 1990; Engle et al. 1996; Schmidt and Wardle 1998; Hoch et al. 2002). Junipers are evergreen species native to the Great Plains, but their historical distribution was limited to rocky outcrops and similar topoedaphic features that limited the spread of fire. Our focus in this chapter is on eastern redcedar, a species that has expanded from the eastern deciduous forests to the west and from isolated refugia along rivers into upland grasslands (Arend 1950).

Size of mature eastern redcedar varies with site, often reaching a height of 15 m on better forest sites (Dirr 1983; Lawson 1990), but trees rarely grow taller than 10 m on upland grassland sites of the Great Plains (Engle and Kulbeth 1992). Encroaching eastern redcedar can rapidly convert grassland to woodland because of crown growth as great as 0.25 m/year (Engle and Kulbeth 1992; Hoch et al. 2002) combined with dense recruitment of individual seedlings enabled by abundant production of a fleshy fruit dispersed by birds (Holthuijzen and Sharik 1985;

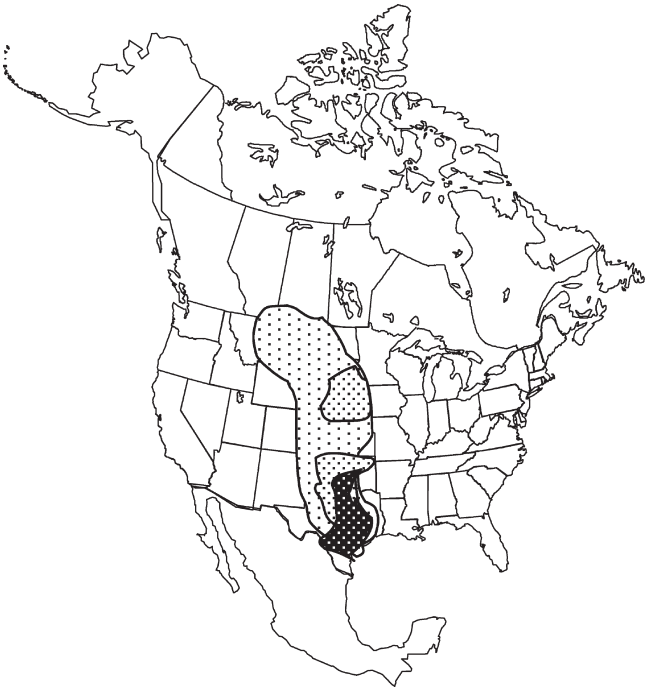

Figure 1 Current distribution of eastern redcedar in Great Plains grasslands (lightly stippled area). The *area densely stippled* has largely been converted to woodland, whereas the *medium-density stippled area* is under threat of conversion to woodland within 10 to 20 years

Horncastle et al. 2004). When eastern redcedar and other species of juniper expand into grasslands, they can greatly alter the biotic and abiotic environment of grassland ecosystems. Their increase reduces the productivity of herbaceous vegetation (Engle et al. 1987; Hoch et al. 2002) and the diversity of grassland plant species, especially beneath the crowns of large trees (Gehring and Bragg 1992; Fuhlendorf et al. 1997; Hoch et al. 2002). Conversion of C_4-dominated grasslands to C_3-dominated woodland greatly alters the hydrological and nutrient cycles of these ecosystems (Thurow and Hester 1997; Norris et al. 2001; Hoch et al. 2002). Found in a wide array of climates and soils (Schmidt and Wardle 2002), eastern redcedar establishes readily and competes effectively in virtually every terrestrial ecosystem in the eastern two-thirds of North America.

Upon Euro-American settlement of the Great Plains, fire suppression in most areas allowed juniper and other fire-limited woody plants to expand their distribution from the east to west and from the rough breaks of drainages to uplands (Figure 2). Trees were planted as windbreaks for homes, to reduce erosion, to enhance wildlife habitat, and to provide relief from the vast open grasslands of the Great Plains (Capel 1988; Knopf 1992; Friedman et al. 1997). Much of the landscape was fragmented by the mid-1900s, but intentional plantings dispersed these woody species throughout the Great Plains, thereby bridging barriers imposed by cropland agriculture (Figure 3). Because native species of juniper are drought tolerant, they persist in most Great Plains environments and, unfortunately, are able to reproduce and expand their range. Tree planting, widely considered a wise conservation act that provided wildlife habitat and greened the landscape, was inconsiderate of obligate grassland wildlife. Government

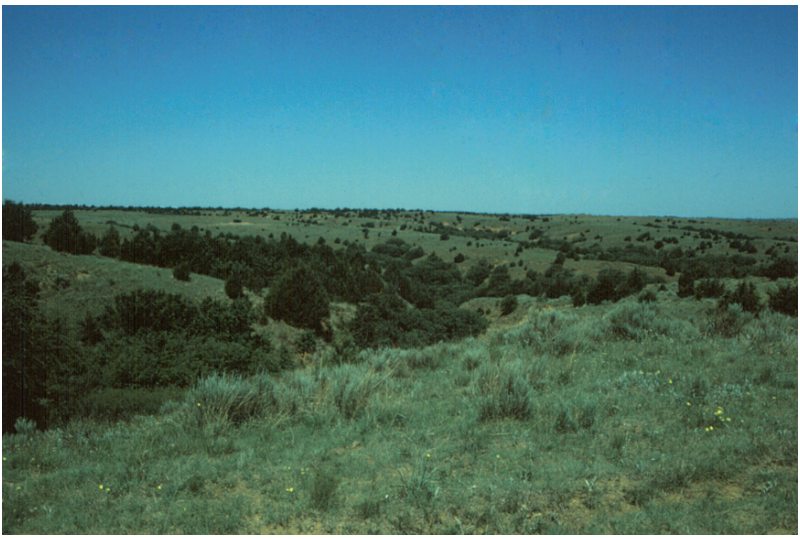

Figure 2 Fire suppression has allowed juniper and other fire-limited woody plants to expand their distribution from east to west and from drainages to uplands, a change ecologically equivalent to glaciation

Figure 3 Intentional tree planting in the Great Plains fragments the remaining patches of grassland and facilitates widespread encroachment. Eastern redcedar is often selected for planting in Great Plains grassland because it is tolerant to a wide range of soil and climate conditions. The species is commonly used for (**a**) living snow fence (eastern redcedar and Russian olive in this case) and (**b**) wildlife habitat improvement. Federal and state programs to control encroachment of eastern redcedar conflict with different programs within the same agency to plant this species as living snow fences within the same counties of Oklahoma. As a wildlife habitat improvement practice, planting eastern redcedar opposes habitat conservation for grassland obligate endemic wildlife

programs to control the expansion of eastern redcedar coexist with other programs in the same agency that plant this species as living snow fences in Oklahoma. A negative feedback of fire suppression resulting from grassland fragmentation leads to reduced herbaceous plant diversity (Leach and Givnish 1996) and an increase in woody plant encroachment, which further fragments grassland (Coppedge et al. 2001b).

Eastern Redcedar Invasion and Grassland Avifauna

Avifauna obligate to the grasslands of the Great Plains is viewed increasingly as important to the U.S. citizenry. Songbirds are considered prime ecological indicators, providing easily observable indices to wildlife habitat structure and ecosystem health (Eyre et al. 1992). Several bird species are locally important to some of the most economically depressed rural economies in the United States. Populations of the greater prairie-chicken, lesser prairie-chicken, and northern bobwhite, the three primary upland game birds of the central and southern Great Plains, are declining across much of their range (Brennan 1991; Church et al. 1993, Silvy and Hagen 2004). With their populations nearing potential listing as endangered, hunting of both species of prairie-chickens has nearly been eliminated (Silvy and Hagen 2004), and hunting remnant populations threatens population viability of all three species in fragmented landscapes (Roseberry and Klemstra 1984:147–148; Woodward et al. 2001; Fuhlendorf et al. 2002; Silvy and Hagen 2004). The increasing rarity of the upland game bird species as well as the entire grassland avifauna has led to increased public and scientific interest in the Great Plains and has fostered interest in development of ecotourism-based enterprises (Henderson 1984; Cordell et al. 1999).

Although causation is debated, obligate grassland birds are the most rapidly declining guild of birds in North America according to the Breeding Bird Survey, an avian survey conducted in late May through June (Bystrak 1981) at more than 3000 sites across North America (Droege 1990). Over the past 30 years these obligate grassland bird species have declined by 70%, and projections indicate the trends will not be reversed. Many factors may be contributing to these declines, but cultivation of grasslands, which in the past contributed to loss of grassland bird breeding habitat, is unlikely to contribute to additional permanent change in land use in the Great Plains (Heimlich and Kula 1991). Recent studies point to the expansion of eastern redcedar as a primary factor responsible for changes in Great Plains avifauna during the past 30 years. Several studies examining the effects of eastern redcedar on the grassland avifauna from regional, landscape, and local spatial scales indicate habitat change resulting from eastern redcedar expansion could extirpate grassland obligate birds from much of the Great Plains.

A recent study documented change in the regional winter bird assemblage associated with differences in regional dominance of eastern redcedar and human population density throughout Oklahoma (Coppedge et al. 2001a). Aside from agricultural activities, Oklahoma landscapes have also experienced significant alteration as a result of low-density urban development, which is highly correlated with the expansion of

eastern redcedar (Coppedge et al. 2001a). Junipers produce prolific fruits that are utilized by frugivorous passerines in winter (Holthuijzen and Sharik 1984, 1985; Chavez-Ramirez and Slack 1996). Therefore, the effects of juniper encroachment on long-term winter abundance patterns of common passerines in Oklahoma should be detectable using data from the Audubon Society Christmas Bird Counts (CBC) (Butcher 1990). The abundance of nine species was found to be significantly related to regional juniper levels (Coppedge et al. 2001a). Three known juniper feeders and seed dispersers, the cedar waxwing (*Bombycilla cedrorum*), eastern bluebird (*Sialia sialis*), and yellow-rumped warbler (*Dendroica coronata*), had significant positive abundance trends with regional juniper levels, as did the ruby-crowned kinglet (*Regulus calendula*). Two other know juniper feeders (American robin, *Turdus migratorius*; blue jay, *Cyanocitta cristata*) exhibited unimodal trends, indicating a preference for regions with moderate juniper levels. Four species, the song sparrow (*Melospiza melodia*), white-crowned sparrow (*Zonotrichia leucophrys*), house sparrow (*Passer domesticus*), and American goldfinch (*Carduelis tristis*), were negatively related to regional juniper encroachment levels (Figure 4). With juniper projected to dominate one-half of the grassland remnants in Oklahoma before 2010, the winter abundance of many frugivorous species that are responsible for spreading juniper seeds will likely increase in Oklahoma and other parts of the southern plains. Conversely, continuation of low-density urban sprawl will accompany juniper encroachment and hinder conservation efforts for many grassland habitats and wildlife already in decline.

A landscape-level study utilized Breeding Bird Survey (BBS) data and a geographic information system to compare bird populations to the dynamics of three landscapes in western Oklahoma over a 30-year period (Figure 5; Coppedge et al. 2001b). Dominance of woody vegetation, composed primarily of eastern redcedar, was the best explanatory variable for shifts in the composition of grassland bird communities. Grassland obligate birds declined as woody plants increased, whereas open habitat generalists, woodland species, and successional shrub species increased in abundance. Many of the grassland obligate bird species are those the BBS indicates are declining (Peterjohn and Sauer 1999).

Yet another landscape-level study sheds light on the influence of juniper on grassland obligate avifauna. This study examined habitat elements associated with the lesser prairie-chicken, a grouse species endemic to prairie and shrubland of the Southern Great Plains (Aldrich 1963; Giesen 1998). Population levels and range have declined by more than 90% from historic levels (Crawford 1980; Taylor and Guthery 1980a; Giesen 1994b). As populations declined precipitously in recent decades (Bailey and Williams 2000; Giesen 2000; Horton 2000; Jensen et al. 2000; Sullivan2000), hunting has been discontinued in Oklahoma and New Mexico (Hagen et al. 2004), and the bird has been considered a "warranted, but was precluded" threatened species by the U.S. Fish and Wildlife Service (Giesen 1998). Previous research, focused primarily on habitat requirements at the local level, demonstrated that the lesser prairie-chicken requires a mosaic of prairie and shrubland habitats dispersed across the landscape, albeit the nature of such dispersion remains unknown (Jones 1963; Riley et al. 1992; Riley and Davis 1993; Giesen

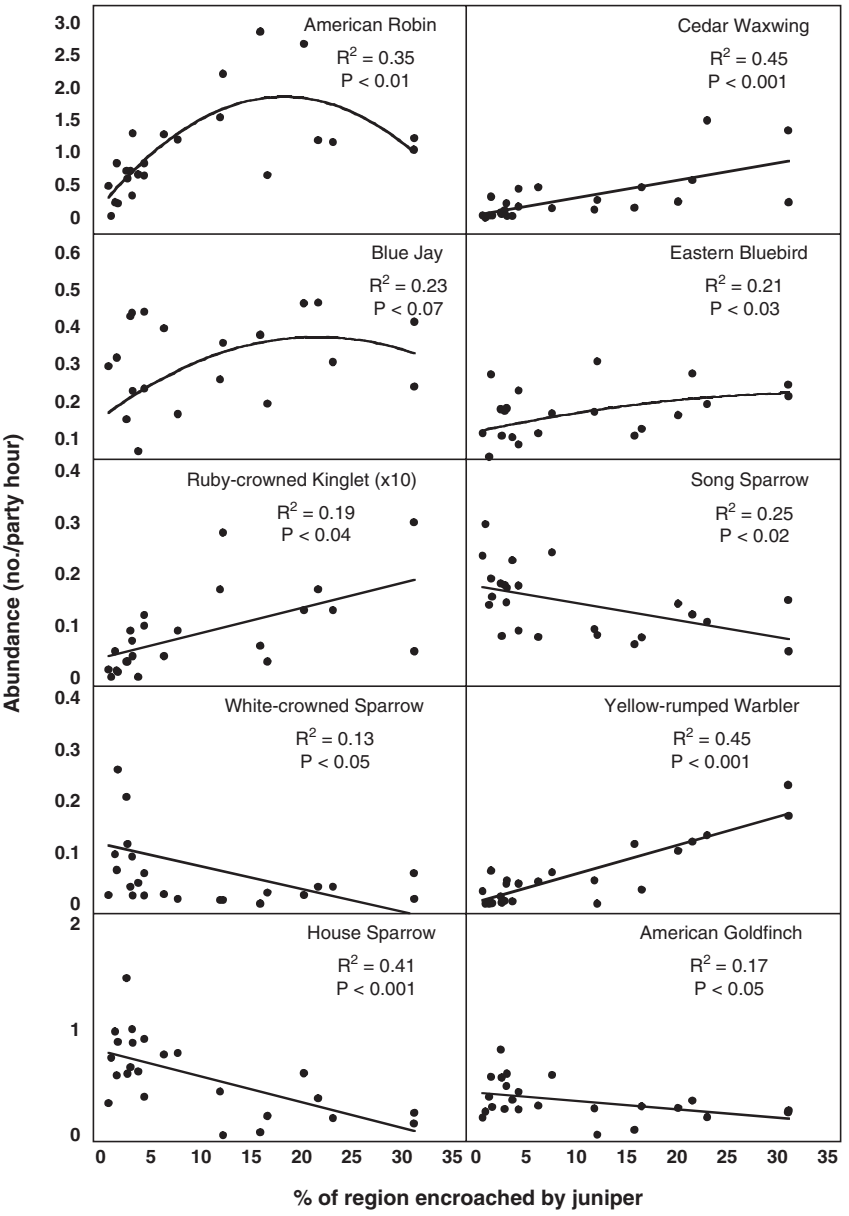

Figure 4 Results of regression models relating mean species abundance of selected birds wintering in Oklahoma to regional encroachment of eastern redcedar for the 1950–1994 time period. (From Coppedge et al. 2001a, with permission from Kluwer Academic Press)

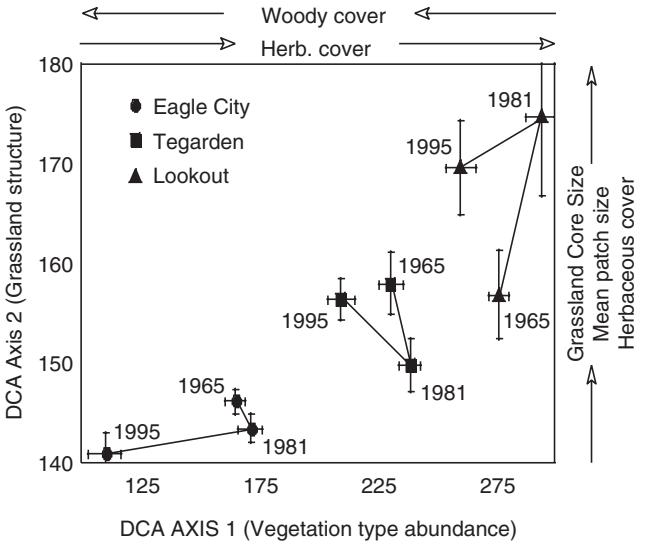

Figure 5 Plot of the results of a detrended correspondence analysis of bird abundance observed on three routes of the North American Breeding Bird Survey. The landscapes surrounding each route varied in proportion of cover of woodlands, primarily composed of eastern redcedar, and fragmented by cropland agriculture. The primary gradient associated with bird community composition was the relative cover of vegetation types, woodland and grassland. (From Coppedge et al. 2001b, copyright Ecological Society of America)

1998). This research also indicated that the lesser prairie-chicken possesses a high degree of site fidelity to habitat surrounding or adjacent to their breeding display grounds (leks), and their home ranges can be several thousand hectares (Taylor and Guthery 1980b; Giesen 1994a; Riley et al. 1994). Several authors have speculated that 1024 to 7238 ha of unfragmented habitat (native grassland and shrubland) might be required to sustain a population, suggesting that populations might be associated with landscape-level structure and patch stability (Davison 1940; Crawford and Bolen 1976; Taylor and Guthery 1980b; Woodward et al. 2001). A study focusing on permanent breeding grounds and the surrounding landscapes found that although cultivation historically fragmented these landscapes, cultivated land had decreased over the past 20 years (Woodward et al. 2001). However, fragmentation continued in recent years because of the increased dominance of trees, primarily eastern redcedar, and decline of some lesser prairie-chicken populations can be attributed to this source of fragmentation (Figure 6).

Coarse-scale habitat features constrain local-level habitat relationships so that the effect of regional juniper expansion is also exhibited at local levels. A study examining the relationship between local habitat structure and bird communities demonstrated that the canopy cover of eastern redcedar explained a greater proportion of the composition of bird communities in southern mixed prairie than did the structure of herbaceous vegetation (Figure 7; Chapman et al. 2004). Structure of

Figure 6 Except for the encroaching eastern redcedar, this shrub-steppe in the western Great Plains provides suitable habitat for lesser prairie-chicken, a grassland obligate species that is declining across its range. Visual cues provided to the birds by the trees might be perceived as unsuitable habitat, perhaps because predators increase with tree encroachment (Bradley and Fagre 1988, Winter et al. 2000)

herbaceous vegetation, manipulated primarily through herbivory and fire, is a key factor in habitat selection by grassland obligate birds in the breeding season (Weins 1974; Cody 1985; Knopf 1996). However, as the canopy cover of eastern redcedar increases, variability in species composition and density decreases, indicating that canopy cover of eastern redcedar will constrain the local influence of herbaceous habitat structure (Figure 8). The practical significance of this is that the application of fire and herbivory, wildlife habitat management practices that ordinarily can be used to enhance habitat in Great Plains grasslands, becomes increasingly influential as eastern redcedar increases in abundance.

Together, these studies indicate encroaching juniper meaningfully influences the avian community at multiple spatial scales. Already declining grassland species decline further as eastern redcedar increases, whereas woodland, shrubland, and some frugivorous species benefit from the presence of this invasive woody species. The expansion of eastern redcedar and other juniper species is at least partially responsible for declining populations of grassland obligate birds. Although an influx of woody vegetation generally increases the resources available to avian communities, it in turn alters avian community composition by attracting avian exotics and habitat generalists and decreasing habitat suitability for endemic and obligate avian grassland species (Blair 1996; Farina 1997; Preiss et al. 1997). The size and diversity of grassland bird communities are already quite low consequent to a limited resource base inherent to North American grasslands because of recurrent

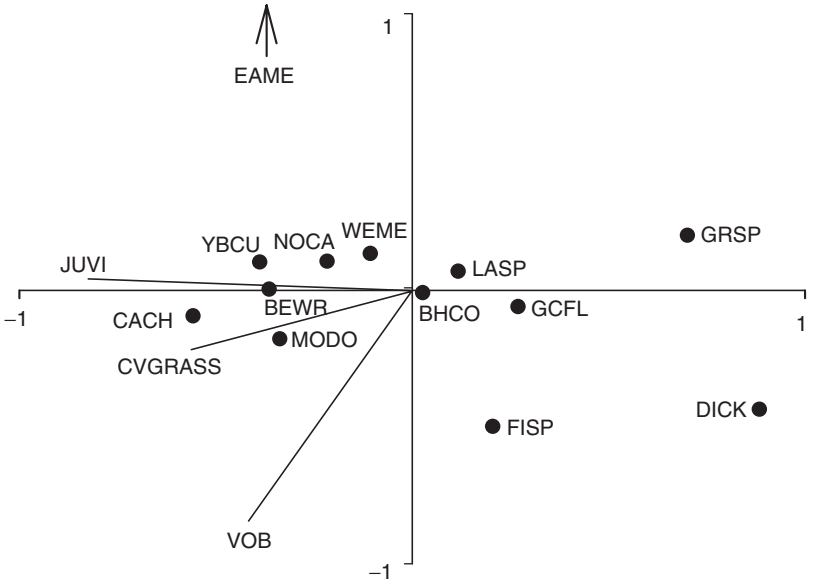

Figure 7 Plot of the results of an ordination (canonical correspondence analysis) relating bird species to habitat variables on sites within the mixed prairie of northwestern Oklahoma. Vectors (*lines with arrows*) show relationships between habitat variables and axes; *length of the vector* indicates the importance of the variable, and *direction* indicates strength of correlation with individual axes. *Axis 1* explains the greatest amount of association between the habitat variables and abundance of bird species, which indicates that eastern redcedar is the primary habitat variable explaining avian species composition. *JUVI*, canopy cover of eastern redcedar; *VOB*, visual obstruction, a measure of vertical structure; *CVGRASS*, coefficient of variability of grass canopy cover, a measure of horizontal structural patchiness; all *four-letter abbreviations* are American Ornithological Union species codes of common bird species of the southern mixed-grass prairie. (From Chapman et al. 2004, copyright Écoscience)

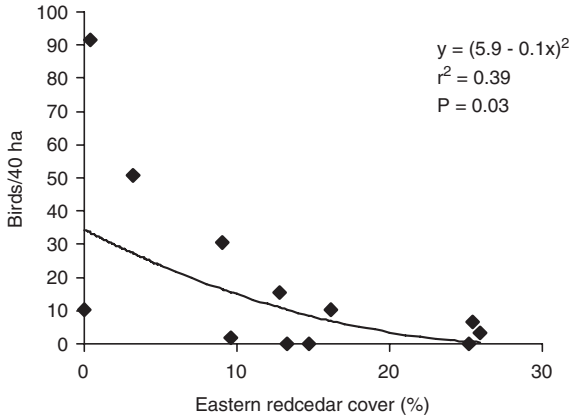

Figure 8 Regression model showing that relative abundance of bird species associated with grassland habitats decreases as canopy cover of eastern redcedar increases. Just as important, variability in bird species composition decreases as canopy cover of eastern redcedar increases, indicating that canopy cover of eastern redcedar constrains the local influence of herbaceous habitat structure created by herbivory and fire. (From Chapman et al. 2004, copyright Écoscience)

drought (Wiens 1974) and fragmentation of grassland habitat (Herkert et al. 2003). In fact, the Great Plains once served as a geographic barrier to woodland avifaunas (Mengel 1970), but westward expansion of species from eastern deciduous forests has been fostered by the development of riparian woodlands along major rivers (Johnson 1994) that provide regional habitat corridors across the Great Plains (Knopf 1986). The mixing of eastern and western avifaunas has resulted in the loss of several subspecific avian forms and the general loss of genetic and community distinctiveness (Rising 1983; Knopf 1986). Using prescribed fire to prevent encroachment of eastern redcedar, and therefore grassland fragmentation and degradation, would contribute significantly to reducing the rates of decline in grassland bird species. Curtailing sponsored, intentional planting of eastern redcedar and other trees by federal and state agencies would also contribute to reducing this decline.

Summary

The Green Glacier or woody plant encroachment into grasslands is creating a 21st-century environmental crisis that might well surpass the ecological impact of the 20th-century Dust Bowl. The Dust Bowl resulted from unwise conversion of large

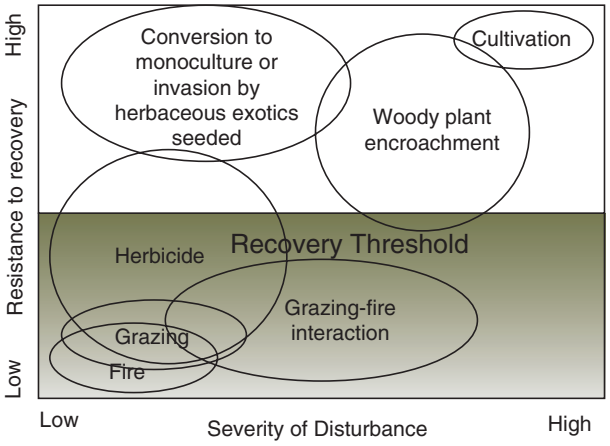

Figure 9 Resistance to recovery of Great Plains grasslands as a function of severity of disturbance. *Circles* indicate the normal bounds of variation in recovery potential for a particular kind of disturbance. The *horizontal midline* indicates the bound above which the grassland will not recover to the state to which it existed before disturbance. Great Plains grasslands evolved with grazing and fire, unlike the anthropogenic disturbances of cultivation and planting of both herbaceous plants and woody plants. Fire exclusion, the result of anthropogenic intervention, also accounts for a current profusion of woody plants in the largely treeless grasslands of the Great Plains

blocks of Great Plains grasslands unsuited to cultivation to cropland agriculture, and it culminated in one of America's most noted environmental disasters. Conversion of native grassland to cropland is no longer the primary threat in the region. A second environmental crisis, the Green Glacier or woody plant encroachment, now accounts for the great majority of land conversion and represents the primary environmental concern for the native grasslands of the Great Plains (Figure 9).The Green Glacier, a present threat perhaps more egregious than the Dust Bowl, has added to the fragmentation accomplished in the original breakout of the prairie sod (Coppedge et al. 2001c). However, in contrast to the original plowing of prairie sod, the Green Glacier is even less selective of sites, and therefore presents conservationists and the general public with perhaps a greater challenge than did the Dust Bowl, which marshaled a national conservation movement for the soil resource.

In this chapter, we used birds as model ecological indicators to quantify the environmental costs of eastern redcedar encroachment into Great Plains grasslands. Other environmental costs will likely be commensurate to the loss incurred by the grassland obligate avifauna. Water yield and water quality will decline with the loss of herbaceous vegetation, human respiratory health will be threatened as eastern redcedar pollen counts increase, and a host of other ecosystem-related goods and services will be negatively affected. Lacking the Black Sunday that caught the nation's attention of the Dust Bowl, we wonder what lever must be tripped before the nation's conservation consciousness is raised on the more insidious Green Glacier.

Acknowledgments This manuscript was funded by the Oklahoma Agricultural Experiment Station (OAES) and was published with the approval of the OAES director.

References

Albertson, F.W., Tomanek, G.W., and Riegel, A. 1957. Ecology of drought cycles and grazing intensity on grasslands of central Great Plains. Ecol. Monogr. 27:27–44.

Aldich, J.W. 1963. Geographic orientation of American *Tetraonidae*. J. Wildl. Manag. 27:529–545.

Anderson, R.C. 1990. The historic role of fire in the North American grassland. In: Fire in the North American tallgrass prairies, eds. S.L. Collins and L.L. Wallace, pp 8–18. Norman, OK: University of Oklahoma Press.

Ansley, J.A., Pinchak, W.E., and Ueckert, D.N. 1995. Changes in redberry juniper distribution in northwest Texas (1948–1982). Rangelands 17:49–53.

Arend, J.L. 1950. Influence of fire and soil on distribution of eastern redcedar in the Ozarks. J. For. 48:129–130.

Axelrod, D.I. 1985. Rise of the grassland biome, central North America. Bot. Rev. 51:163–202.

Bailey, J.A., and Williams, S.O., III. 2000. Status of the lesser prairie-chicken in New Mexico. Prairie Nat. 32:157–168.

Baltensperger, B.H. 1979. Agricultural adjustments to Great Plains drought, the Republican Valley, 1870–1900. In: The Great Plains, environment and culture, eds. B.W. Blouet and F.C. Luebke, pp 43–59. Lincoln, NE: University of Nebraska Press.

Bedenbaugh, E.J. 1988. History of cropland set aside programs in the Great Plains. In: Impacts of the conservation reserve program in the Great Plains, ed. J.E. Mitchell, pp 14–17. General

technical report RM-158. Fort Collins, CO: United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.
Blair, R.B. 1996. Land use and avian species diversity along an urban gradient. Ecol. Appl. 6:506–519.
Borchert, J.R. 1950. The climate of the central North American grassland. Ann. Assoc. Am. Geogr. XL:1–39.
Bradley, L.C., and Fagre, D.B. 1988. Coyote and bobcat response to integrated ranch management practices in south Texas. J. Range. Manag. 41:322–327.
Brennan, L.A. 1991. How can we reverse the northern bobwhite population decline? Wildl. Soc. Bull. 19:544–555.
Briggs, J.M., Knapp, A.K., Blair, J.M., Heisler, J.L., Hoch, G.A., Lett, M.S., and McCarron, J.K. 2005. An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. BioScience 55:243–254.
Butcher G.S. 1990. Audubon Christmas bird counts. In: Survey designs and statistical methods for the estimation of avian population trends, eds. J.R Sauer and S. Droege, pp 5–13. Biological report 90. Washington, DC: United States Department of the Interior.
Bystrak, D. 1981. The North American Breeding Bird Survey. In: Estimating numbers of terrestrial birds, eds. C.J. Ralph and J.M. Scott. Studies Avian Biol. 6:34–41.
Capel, S.W. 1988. Design of windbreaks for wildlife in the Great Plains of North America. Agric. Ecosyst. Environ. 22/23:337–347.
Chapman, R.N., D.M. Engle, R.E. Masters, and Leslie, D.M., Jr. 2004. Tree invasion constrains the influence of herbaceous structure in grassland bird habitats. Écoscience 11:55–63.
Chavez-Ramirez, F., and Slack, R.D. 1996. Winter phenology and frugivory of American robins and cedar waxwings on the Edwards Plateau of central Texas. Tex. J. Sci. 48:129–136.
Church, K.E., Sauer, J.R., and Droege, S. 1993. Population trends of quails in North America. Proc. Natl. Quail Symp. 3:44–54.
Cody, M.L. 1985. Habitat selection in grassland and open-country birds. In: Habitat selection in birds. ed. M.L. Cody, pp 191–226. Orlando: Academic Press.
Coppedge, B.R., Engle, D.M., Fuhlendorf, S.D., Masters, R.E., and Gregory, M.S. 2001a. Urban sprawl and juniper encroachment effects on abundance of wintering passerines in Oklahoma. In: Avian ecology and conservation in an urbanizing world. eds. J.M. Marzluff, R. Bowman, and R. Donnelly, pp 225–242. Norwell, MA: Kluwer.
Coppedge, B.R., Engle, D.M., Masters, R.E., and Gregory, M.S. 2001b. Avian response to landscape change in fragmented Southern Great Plains grasslands. Ecol. Appl. 11:47–59.
Coppedge, B.R., Engle, D.M., Fuhlendorf, S.D., Masters, R.E., and Gregory, M.S. 2001c. Landscape cover type and pattern dynamics in fragmented southern Great Plains grasslands, USA. Landsc. Ecol. 16:677–690.
Cordell, H.K., McDonald, B.L., Teasley, R.J., Bergstrom, J.C., Martin, J., Bason, J., and Leeworthy, V.R. 1999. Outdoor recreation participation trends. In: Outdoor recreation in American life: a national assessment of demand and supply trends compared, ed. H.K. Cordell. Champaign: Sagamore.
Coupland, R.T. 1992. Overview of the grasslands of North America. In: Ecosystems of the world: natural grasslands, vol 8A, ed. R.T. Coupland, pp 147–150. Amsterdam: Elsevier.
Crawford, J.A. 1980. Status, problems, and research needs of the lesser prairie-chicken. In: Proceedings, prairie grouse dymposium, eds. P.A. Vohs and F.L. Knopf, pp 1–7. Stillwater, OK: Oklahoma State University.
Crawford, J.A., and Bolen, E.G. 1976. Effects of land use on lesser prairie-chickens in Texas. J. Wildl. Manag. 40:96–104.
Daubenmire, R.F. 1978. Plant geography. New York: Academic Press.
Davison, V.E. 1940. An eight year census of lesser prairie-chickens. J. Wildl. Manag. 4:55–62.
Dirr, M.A. 1983. Manual of woody landscape plants. Champaign: Stipes.
Droege, S. 1990. The North American breeding bird survey. In Survey designs and statistical methods for the estimation of avian population trends, eds. J.R. Sauer and S. Droege, pp 1–4.

Biological report 90(1). Washington, DC: United States Department of the Interior, Fish and Wildlife Service.
Engle, D.M., and Kulbeth, J.D. 1992. Growth dynamics of eastern redcedar at three locations in Oklahoma. J. Range. Manag. 45:301–305.
Engle, D.M., Stritzke, J.F., and Claypool, P.L. 1987. Herbage standing crop around eastern redcedar trees. J. Range. Manag. 40:237–239.
Engle, D.M., Bidwell, T.G., and Moseley, M.E. 1996. Invasion of Oklahoma rangelands and forests by eastern redcedar and ashe juniper. Circular E-947. Stillwater, OK: Cooperative Extension Service, Oklahoma State University.
Epstein, H.E., Lauenroth, W.K., Burke, I.C., and Collins, D.P. 1996. Ecological response of dominant grasses along two climatic gradients in the Great Plains of the United States. J. Veg. Sci. 7:777–788.
Eyre, M.D., Rushton, S.P., Young, A.G., and Hill, D. 1992. Land cover and breeding birds. In: Land use change: the causes and consequences, ed. M.C. Whitby, pp 131–136. London: ITE Symposium 27.
Farina, A. 1997. Landscape structure and breeding bird distribution in a sub-Mediterranean agro-ecosystem. Landsc. Ecol. 12:365–378.
Flores, D.L. 1996. A long love affair with an uncommon country: environmental history of the Great Plains. In: Prairie conservation: preserving North America's most endangered ecosystem, eds. F.B. Samson and F.L. Knopf, pp 3–17. Washington, DC: Island Press.
Friedman, J.M., Scott, M.L., and Auble, B.T. 1997. Water management and cottonwood forest dynamics along prairie streams. In: Ecology and conservation of Great Plains vertebrates, vol 125, eds. F.L. Knopf and F.B. Samson, pp 49–71. New York: Springer-Verlag.
Fuhlendorf, S.D., Smeins, F.E., and Grant, W.E. 1996. Simulation of a fire-sensitive ecological threshold: a case study of Ashe juniper on the Edwards Plateau of Texas, USA. Ecol. Model. 90:245–255.
Fuhlendorf, S.D., Smeins, F.E., and Taylor, C.A. 1997. Browsing and tree size influences on Ashe juniper understory. J. Range. Manag. 50:507–512.
Fuhlendorf, S.D., Woodward, A.J.W., Leslie, D.M., Jr., and Shackford, J.S. 2002. Multi-scale effects of habitat loss and fragmentation on lesser prairie-chicken populations of the US Southern Great Plains. Landsc. Ecol. 17:617–628.
Giesen, K.M. 1994a. Movements and nesting habitat of lesser prairie-chicken hens in Colorado. Southwest. Nat. 39:96–98.
Giesen, K.M. 1994b. Breeding range and population status of lesser prairie-chickens in Colorado. Prairie Nat. 26:175–182.
Giesen, K.M. 1998. Lesser prairie-chicken (*Tympanuchus pallidicinctus*). In: The birds of North America, eds. A. Poole and F. Gill. Account no. 364. Philadelphia: Academy of Natural Sciences; Washington, DC: American Ornithologists' Union.
Giesen, K.M. 2000. Population status and management of lesser prairie-chicken in Colorado. Prairie Nat. 32:137–148.
Gehring, J.L., and T.B. Bragg. 1992. Changes in prairie vegetation under eastern redcedar (*Juniperus virginiana*) in an eastern Nebraska bluestem prairie. Am. Midl. Nat. 128:209–217.
Glantz, M.H. 1994. Drought, desertification and food production. In: Drought follows the plow, ed. M.H. Glantz, pp 9–30. New York: Cambridge University Press.
Hagan, C.A., Jamison, B.E., Giesen, K.M., and Riley, T.Z. 2004. Guidelines for managing lesser prairie-chicken populations and their habitats. Wildl. Soc. Bull. 32:69–82.
Heimlich, R.E., and Kula, O.E. 1991. Economics of livestock and crop production on post-CRP lands. In: The conservation reserve: yesterday, today and tomorrow, eds. L.A. Joyce, J.E. Mitchell, and M.D. Skold, pp 11–23. General technical report RM-203. Fort Collins, CO: United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.
Henderson, F.R. 1984. Guidelines for increasing wildlife on farms and ranches: with ideas for supplemental income sources for rural families. Great Plains Agricultural Council, Wildlife

Resources Committee. Manhattan, KS: Cooperative Extension Service, Kansas State University.
Herkert , J.R., Reinking, D.L., Wiedenfeld, D.A., Winter, M., Zimmerman, J.L., Jensen, W.E., Finck, E.J., Koford, R.R., Wolfe, D.H., Sherrod, S.K., Jenkins, M.A., Faaborg, J., and Robinson, S.K. 2003. Effects of prairie fragmentation on the nest success of breeding birds in the midcontinental United States. Conserv. Biol. 17:587–594.
Hoch, G.A., Briggs, J.M., and Johnson, L.C. 2002. Assessing the rate, mechanism and consequences of conversion of tallgrass prairie to *Juniperus virginiana* forest. Ecosystems 6:578–586.
Holthuijzen, A.M.A., and Sharik, T.L. 1984. Seed longevity and mechanisms of regeneration of eastern redcedar (*Juniperus virginiana* L.). Bull. Torrey Bot. Club 111:153–158.
Holthuijzen, A.M.A., and Sharik, T.L. 1985. The avian seed dispersal system of eastern redcedar (*Juniperus virginiana* L.). Can. J. Bot. 63:1508–1515.
Horncastle, V.J., Hellgren, E.C., Mayer, P.M., Engle, D.M., and Leslie, D.M., Jr. 2004. Differential consumption of eastern redcedar (*Juniperus virginiana*) by avian and mammalian guilds: implications for tree invasion. Am. Midl. Nat. 152:255–267.
Horton, R.E. 2000. Distribution and abundance of lesser prairie-chicken in Oklahoma. Prairie Nat. 32:189–195.
Jensen, W.E., Robinson, D.A., Jr., and Applegate, R.D. 2000. Distribution and population trend of lesser prairie-chicken in southwestern Kansas. Prairie Nat. 32:169–175.
Joern, A., and Keeler, K. 1995. The changing prairie: North American grasslands. New York: Oxford University Press.
Johnson, W.C. 1994. Woodland expansion in the Platte River, Nebraska: pattern and causes. Ecol. Monogr. 64:45–84.
Jones, R.E. 1963. Identification and analysis of lesser and greater prairie-chicken habitat. J. Wildl. Manag. 27:757–778.
Joyce, L.A. 1989. An analysis of the range forage situation in the United States: 1989–2040. General technical report RM-180. Fort Collins, CO: United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.
Knopf, F.L. 1986. Changing landscapes and the cosmopolitanism of eastern Colorado avifauna. Wildl. Soc. Bull. 14:132–142.
Knopf, F.L. 1992. Faunal mixing, faunal integrity, and the biopolitical template for diversity conservation. Trans. N. Am. Wildl. Nat. Res. Conf. 57:330–342.
Knopf, F.L. 1994. Avian assemblages on altered grasslands. Studies Avian Biol. 15:247–257.
Knopf, F.L. 1996. Prairie legacies—birds. In: Prairie conservation. preserving North America's most endangered ecosystem, eds. F.B. Samson and F.L. Knopf, pp 135–148. Washington, DC: Island Press.
Kuchler, A.W. 1964. Potential natural vegetation of the conterminous United States. Special publication no. 36. Washington, DC: American Geographical Society.
Lawson, E.R. 1990. *Juniperus virginiana* L. eastern redcedar. In: Silvics of North America, vol 1. Conifers, eds. R.M. Burns and B.H. Honkala, pp 131–140, Agriculture handbook 654. Washington, DC: United States Department of Agriculture, Forest Service.
Laycock, W.A. 1988. History of grassland plowing and grass planting on the Great Plains. In: Impacts of the conservation reserve program in the Great Plains, ed. J.E. Mitchell, pp 3–8. General technical report RM-158. Fort Collins, CO: United States Department of Agriculture, Forest Service.
Leach, M.K., and Givnish, T.J. 1996. Ecological determinants of species loss in remnant prairies. Science 273:1555–1558.
Licht, D.S. 1997. Ecology and economics of the Great Plains. Lincoln, NE: University of Nebraska Press.
Mack, R.N., and Thompson, J.N. 1982. Evolution in steppe with few large, hooved mammals. Am. Nat. 119:757–773.
McDonald, J.N. 1981. North American bison: their classification and evolution. Berkeley: University of California Press.

Mengel, R.M. 1970. The North American central plains as an isolating agent in bird speciation. In: Pleistocene and recent environments of the central Great Plains, eds. W. Dort and J.K. Jones, Jr., pp 279–340. Lawrence, KS: University of Kansas Press.

Mitchell, J.E., Louda, S.M., and Gillam, B. 1999. Background and synopsis: symposium on the Great Plains grasslands at the millennium. Great Plains Res. 9:211–222.

Norris, M.D., Blair, J.M., Johnson, L.C., and McKane, R.B. 2001. Assessing changes in biomass, productivity, and C and N stores following *Juniperus virginiana* forest expansion into tallgrass prairie. Can. J. For. Res. 31:1940–1946.

O'Neill, R.V., Hunsaker, C.T., Jones, K.B., Riitters, K.H., Wickham, J.D., Schwartz, P.M., Goodman, I.A., Jackson, B.L., and Baillargeon, W.S. 1997. Monitoring environmental quality at the landscape scale. Bioscience 47:513–519.

Peterjohn, B.G., and Sauer, J.R. 1999. Population status of North American grassland birds. Studies Avian Biol. 19:27–44.

Pielou, E.C. 1992. After the Ice Age: the return of life to glaciated North America. Chicago: University of Chicago Press.

Preiss, E., Martin, J.L., and Debussche, M. 1997. Rural depopulation and recent landscape changes in a Mediterranean region: consequences to the breeding avifauna. Landsc. Ecol. 12:51–61.

Pyne, S.J. 1982. Fire in America: a cultural history of wildland and rural fire. Princeton, NJ: Princeton University Press.

Riley, T.Z., and Davis, C.A. 1993. Vegetative characteristics of lesser prairie-chicken brood foraging sites. Prairie Nat. 25:243–248.

Riley, T.Z., Davis, C.A., Ortiz, M., and Wisdom, M.J. 1992. Vegetative characteristics of successful and unsuccessful nests of lesser prairie chickens. J. Wildl. Manag. 56:383–387.

Riley, T.Z., Davis, C.A., Candelaria, M.A., and Suminski, H.R. 1994. Lesser prairie-chicken movements and home ranges in New Mexico. Prairie Nat. 26:183–186.

Rising, J.D. 1983. The Great Plains hybrid zones. Curr. Ornithol. 1:131–157.

Roseberry, J.L., and Klimstra, W.D. 1984. Population ecology of the bobwhite. Carbondale, IL: Southern Illinois University Press.

Sala, O.E., Parton, W.J., Joyce, L.A., and Lauenroth, W.K. 1988. Primary production of the central grassland region of the United States: spatial pattern and major controls. Ecology 69:40–45.

Sampson, F., and Knopf, F. 1994. Prairie conservation in North America. Bioscience 44:418–421.

Schmidt, T.L., and Wardle, T.D. 1998. The forest resources of Nebraska. Research paper NC-332. St. Paul, MN: United States Department of Agriculture, Forest Service, North Central Research Station.

Schmidt, T.L., and Wardle, T.D. 2002. Impact of pruning eastern redcedar (*Juniperus virginiana*). West. J. Appl. For. 17:189–193.

Silvy, N.J., and Hagen, C.A. 2004. Introduction: management of imperiled prairie grouse species and their habitat. Wildl. Soc. Bull. 32:2–5.

Sopuck, R.D. 1995. Sustaining the Great Plains ecosystem: integrating people economics and the landscape. In: Conservation of Great Plains ecosystems: current science, future options, eds. S.R. Johnson and A. Bouzaher, pp 83–95. Amsterdam: Kluwer.

Stebbins, G.L. 1981. Coevolution of grasses and herbivores. Ann. Mo. Bot. Gard. 68:75–86.

Sullivan, R.M., Hughes, J.P., and Lionberger, J.E. 2000. Review of the historical and present status of the lesser prairie-chicken (*Tympanuchus pallidicinctus*) in Texas. Prairie Nat. 32:178–188.

Taylor, M.S., and Guthery, F.S. 1980a. Status, ecology, and management of the lesser prairie-chicken. General technical report RM-77. Fort Collins, CO: United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Taylor, M.S., and Guthery, F.S. 1980b. Fall-winter movements, ranges, and habitat use of lesser prairie-chickens. J. Wildl. Manag. 44:521–524.

Thurow, T.L., and Hester, J.W. 1997. How an increase or reduction in juniper cover alters rangeland hydrology. In: 1997 juniper symposium, ed. C.A. Taylor, pp 4.9–4.22. Technical report 97-1. Sonora, TX: Texas Agricultural Experiment Station.

Van Haverbeeke, D.F., and King, R. 1990. Genetic variation in Great Plains *Juniperus*. Research paper RM-292. Fort Collins, CO: United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Vickery, P.D., Tubaro, P.L., Da Silva, J.M.C., Peterjohn, B.G., Herkert, J.R., and Cavalcanti, R,B. 1999. Conservation of grassland birds in the western hemisphere. Studies Avian Biol. 19:2–26.

Wiens, J.A. 1974. Habitat heterogeneity and community structure in North American grassland birds. Am. Midl. Nat. 91:195–213.

Winter, M., Johnson, D.H., and Faaborg, J. 2000. Evidence for edge effects on multiple levels in tallgrass prairie. Condor 102:256–266.

Woodward, A.J., Fuhlendorf, S.D., Leslie, D.M., Jr., and Shackford, J. 2001. Influence of landscape composition and change on lesser prairie-chicken (*Tympanuchus pallidicinctus*) populations. Am. Midl. Nat. 145:261–274.

Wright, H.E., Jr. 1970. Vegetational history of the Central Plains. In: Pleistocene and recent environments of the Central Great Plains, eds. W. Dort and J.K. Jones, Jr., pp 157–172. Lawrence, KS: University of Kansas Press.